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SHELL ENTRY AND SHELL SELECTION OF HYDROID-COLONIZED SHELLS BY THREE SPECIES OF HERMIT CRABS FROM THE NORTHERN GULF OF MEXICO*

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ABSTRACT

The shell entry and shell selection of hydroid-colonized (either *Hydractinia echinata* or *Podocoryne selena*) shells by two populations each of *Pagurus pollicaris, P. longicarpus,* and *Clibanarius vittatus* were observed under various conditions. All three species either initially chose or subsequently switched into bare shells, even in the presence of a predator. The population of *P. pollicaris* where *Octopus joubini* was more abundant initially selected hydroid-colonized shells more frequently in one experiment than did the other population of crabs. The general avoidance of hydroid-colonized shells is probably due to the crabs' being stung by nematocysts.

INTRODUCTION

Because hermit crabs live in empty gastropod shells, their shell selection can be viewed as a form of habitat selection (Conover, 1978). Therefore, just as many other animals selectively choose their habitat (Cox *et al.*, 1976), hermit crabs nonrandomly select their gastropod shells. Most studies involving shell selection by hermit crabs have focused on the significance of various shell characteristics such as species, volume, weight, aperture size, and morphology (Reese, 1962, 1963; Völker, 1967; Markham, 1968; Childress, 1972; Kuris and Brody, 1976; Conover, 1978).

Organisms that colonize the exterior surface of the gastropod shell also affect shell selection (Conover, 1976). In particular, epifaunal hydroid colonies (*e.g., Hydractinia echinata*) typically form encrusting mats on the shells. Certain hermit crabs select hydroid-colonized shells more often than bare shells when given a choice. For example, Jensen (1970) demonstrated that *Pagurus bernhardus* preferred *Hydractinia*-colonized shells to bare shells. Similarly, Grant and Ulmer (1974) showed that *P. acadianus* also preferred *Hydractinia*-colonized shells.

Apparently, however, the preference for hydroid-colonized shells can vary within a species. For example, differences in shell selection have been reported for the hermit crabs *P. pollicaris* and *P. longicarpus,* both of which are common along the North American coasts of the Atlantic Ocean and the Gulf of Mexico. *Pagurus pollicaris* preferred hydroid-colonized shells in studies by Wright (1973), Conover (1976), and Mercando and Lytle (1980). Mills's (1976a) preliminary observations, however, showed that *P. pollicaris* rejects hydroid-colonized shells. Similarly, *P. longicarpus* preferred hydroid-colonized shells in studies by Wright (1973) and Conover (1976), but both Mills (1976a) and Mercando and Lytle (1980) reported that it usually rejected them.

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Although the differences in the above studies may be due, in part, to differing laboratory conditions, the hermit crabs in each study were collected from different localities. Therefore, it is possible that behavioral differences exist between populations of these hermit crabs. Abrams (1978) found that one population of the terrestrial hermit crab *Coenobita compressus* selected larger shells than another population. In addition, Bertness (1982) showed that two populations each of the hermit crabs *Clibanarius albidigitus* and *Calcinus obscurus* differed in shell-species selection. The populations of the two species located where predation pressure was higher selected shells that would minimize predation pressure (Bertness, 1982). Similarly, Scully (1979) found that two populations of *P. longicarpus* chose different sized shells. He also suggested that physical differences between the two collection sites affected the hermit crabs' shell preference.

The preference of some hermit crabs for and the avoidance by others of hydroid-colonized shells may allow coexistence of similar-sized species. Although Grant and Ulmer (1974) found that *P. acadianus* preferred hydroid-colonized shells, the closely related *P. pubescens,* which is sympatric with *P. acadianus,* preferred bare shells. This difference in shell selection could serve to separate resources (shells) and allow these two species to coexist (Grant and Ulmer, 1974). Similarly, Wright (1973) reported that *Clibanarius vittatus,* which is a competitive dominant over *P. pollicaris* (Wright, 1973), prefers shells without hydroids. He found that when *C. vittatus* contacted the hydroid colony it was apparently stung and avoided any further contact with the hydroid. Wright (1973) never observed *P. pollicaris* or *P. longicarpus,* both of which selected shells with hydroids, to behave as if stung. Wright (1973) suggests that because *Pagurus* occasionally eat the hydroid's polyps, this diet might somehow provide *Pagurus* protection from the cnidae, allowing them to inhabit the hydroid-colonized shell.

The avoidance of hydroid-colonized shells may be due, in part, to the effect on the hermit crab of contact with specialized dactylozooid polyps. These coiled polyps, located at the aperture of the shell, have been described as being "defensive" (Schifjsma, 1935; Stokes, 1974a, b). When the colony is mechanically or electrically disturbed, they uncoil and lash down toward the lumen of the shell (Schifjsma, 1935; Stokes, 1974a, b; Mills, 1976a). During shell entry, a hermit crab would no doubt contact these dactylozooid polyps and, if stung, might make no further attempt to enter the shell.

In the present study, the shell entry and shell selection of hydroid-colonized shells by *P. pollicaris, P. longicarpus,* and *C. vittatus,* all from the northeastern Gulf of Mexico, were observed under various conditions and compared with previous studies. Tests were performed to determine whether cnidae from the dactylozooid polyps discharge onto the surface of the hermit crabs. In addition, the shell selection of two populations for each of the three species was tested. The results of this work show that all three species of hermit crabs either initially choose or subsequently switch into bare shells, even when a predator (a stone crab or octopus) is present. Some populational differences in shell selection existed with *P. pollicaris.* The rejection of hydroid-colonized shells may be due to the crabs' being stung by cnidae from the dactylozooid polyps, because cnidae do discharge onto the hermit crabs.

MATERIALS AND METHODS

All of the animals were kept in closed-system aquaria in the laboratory at the Florida State University, Tallahassee, Florida. The hermit crabs *P. pollicaris* Say, *P. longicarpus* Say, *Clibanarius vittatus* (Bosc), and the stone crab *Menippe mercenaria* (Say) were collected from two intertidal sites in the northeastern Gulf of Mexico at depths less than 2 meters. One locality was near the Florida State University Marine Laboratory (FSUML), Turkey Point, Florida, about 45 miles south of Tallahassee, Florida. The other locality was in St. Joseph Bay adjacent to Port St. Joe, Florida, and about 50 miles west of the FSUML. These two sites differed in that the salinity at the FSUML fluctuated because of freshwater runoff from a nearby creek. The salinity in St. Joseph Bay remained constant at 30–31‰. *Octopus joubini* Robson was collected from St. Joseph Bay, where it is very common (*cf.* Mather, 1972; Butterworth, 1982). *Octopus joubini* is uncommon near the FSUML site (pers. obs.; P. Wilber, Florida State University, pers. comm.). Nearly every *P. pollicaris* was a male. The sex ratios of both *P. longicarpus* and *C. vittatus* were approximately 50:50 male:female.

All of the hermit crabs and the stone crabs were fed Tetra Min flaked fish food. *Octopus joubini* was fed fiddler crabs (*Uca* sp.) and small hermit crabs (*Pagurus* sp.). The shell of the gastropod *Polinices duplicatus* (Say) was used in all of the experiments. In addition, the living hydroid (either *Hydractinia echinata* (Fleming) or *Podocoryne selena* Mills) was used when it was on *P. duplicatus* shells and covered over 90% of the shell's exterior surface. Both species of hydroid commonly occur in the two localities discussed above, but cannot always be clearly distinguished unless in the appropriate reproductive condition (*cf.* Mills, 1976b).

Shell entry of hydroid-colonized shells

We removed hermit crabs from their shells by stroking the crab's abdomen with a flexible plastic cord inserted through a hole drilled in the shell. Each naked hermit crab was placed in a finger bowl filled with sea water, and a hydroid-colonized shell was added to the bowl, with its aperture down. The behavior of the hermit crab was observed. The initial contact was observed closely to determine whether the crab responded as if stung. A sting response was defined generally as a rapid movement of a body part or the whole crab away from the hydroid following contact with one or more polyps. For example, if one of the hermit crab's antennae touched the hydroid and the crab quickly jerked the antenna away, this action was considered a sting response.

Cnida discharge tests

When *P. pollicaris* that live in hydroid-colonized shells retreat into the shells, their eyestalks, antennules, antennae, and chelipeds eventually contact the dactylozooid polyps. Therefore, sensory hairs from the carpus of the cheliped were removed with forceps, stained with 1% Toluidine blue solution, and then examined under a light microscope to determine whether cnidae had discharged onto them (Fig. 1). Ten sensory hairs were removed from each of ten *P. pollicaris*, and the number of cnidae on them was counted. The sensory hairs were chosen rather than the eyestalks, antennules, or antennae because of their small size (which makes them suitable for staining and counting cnidae) and the large number present on the appendages. Furthermore, these sensory hairs are usually associated with sensory endings (Shelton and Laverack, 1970). If the hermit crabs are stung by the hydroids, then the sensory hair is probably at least one of the sites where the stinging stimulus is received and transmitted.

Ten sensory hairs were also removed from each of ten *P. pollicaris* and five *C. vittatus* and rubbed along the fringe of dactylozooids, four times (to ensure contact), from one side of the lip of the shell to the other. These sensory hairs were also stained

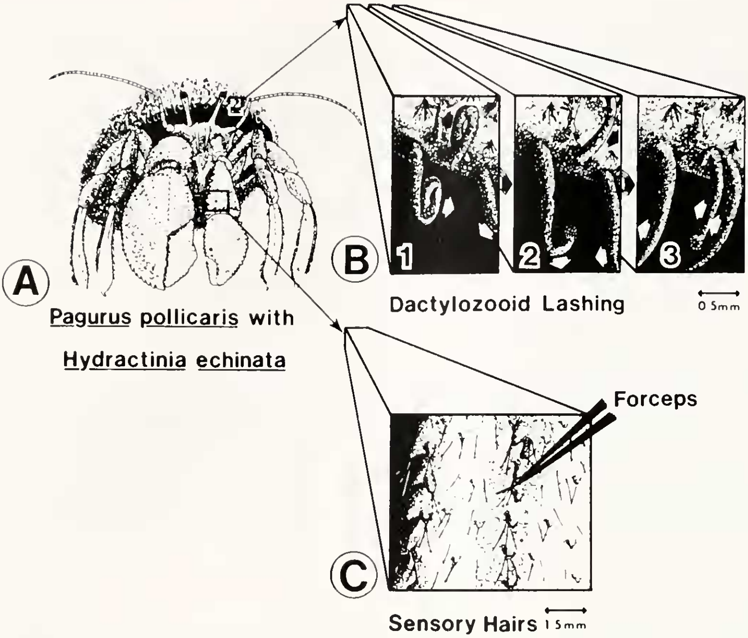

FIGURE 1. The hermit crab *Pagurus pollicaris* inhabiting a *Polinices duplicatus* shell that is colonized by the hydroid *Hydractinia echinata* (A). The dactylozooid polyps of the hydroid uncoil and lash downward when the colony is disturbed (B). Sensory hairs from the carpus of *P. pollicaris* are removed (C) and examined under a light microscope for the dactylozooid's cnidae.

with a 1% Toluidine blue solution and examined under a light microscope to count the cnidae.

In all of the above tests, sensory hairs approximately 3 mm in length were used.

Shell preference tests

Two populations (one from the FSUML and the other from St. Joseph Bay) of each of the hermit crabs, *P. pollicaris, P. longicarpus,* and *C. vittatus,* were used in the following experiments, unless stated otherwise.

Experiment 1. A naked hermit crab was placed in a 1-liter aquarium with two *Polinices duplicatus* shells of the same size (same shell aperture ± 1 mm). One shell, however, was colonized by a hydroid while the other was bare. The shell choice of the hermit crab was recorded at the ends of two observation periods: (1) at five minutes and (2) at eight hours. Two observations were made to determine whether the hermit crabs stay in the shell they choose first.

Control 1. This experiment was done to determine whether there were additional factors associated with hydroid-colonized shells that caused the hermit crabs either to select or avoid these shells. Therefore, the hydroid colonies were scraped off of the shells with a knife. The naked hermit crabs were then given a choice between the shells that had had their hydroids scraped off and shells that were originally bare. The two shells were the same size. The shell choice of the hermit crab was recorded at five minutes and eight hours.

Experiment 2. Hazlett (1980) has argued that the degree of avoidance of hydroid-colonized shells by hermit crabs may be overestimated using naked crabs. Therefore, in an experiment designed to determine whether the naked hermit crabs select hydroid-colonized shells differently from hermit crabs in shells, the naked crabs were first allowed to enter *P. duplicatus* shells in which only their abdomen could fit. They were then given a choice between hydroid-colonized shells and bare shells of the same size. After the hermit crab entered the small shell, it was then placed in a 1-liter aquarium, and its shell choice was recorded after five minutes and after eight hours.

Control 2. Again, the naked hermit crabs were first allowed to enter small *P. duplicatus* shells. This time, however, the hydroids were scraped off of the shells as was done in Control 1 to determine whether additional factors (other than the hydroid) associated with the hydroid-colonized shells affect the shell choice of the hermit crabs. The hermit crab was then given a choice between a shell with its hydroid colony removed and a shell of the same size that was originally bare. The shell choice of the hermit crab was recorded at five minutes and at eight hours.

Experiment 3. The naked hermit crab was placed in a 1-liter aquarium with one hydroid-colonized shell. Observations were made at five minutes and eight hours to determine whether the hermit crab entered the shell.

Experiment 4. In an experiment to reveal shell selection behavior in the presence of a crustacean predator, the naked hermit crab was placed in a 4-liter aquarium with the stone crab *M. mercenaria* present. The hermit crab was given a choice between hydroid-colonized shells and bare shells. The two shells were the same size. The shell choice of the hermit crab was recorded at five minutes and at eight hours.

Experiment 5. In an experiment designed to compare shell selection behavior in the presence of a cephalopod predator, the naked hermit crab was placed in a 4-liter aquarium with the octopus *O. joubini.* The hermit crab was given a choice between hydroid-colonized shells and bare shells. The two shells were the same size. The shell choice of the hermit crab was recorded after five minutes and after eight hours.

RESULTS

Shell entry of hydroid-colonized shells

Pagurus pollicaris usually used its antennae to make initial contact with the hydroid, but did not respond as if stung (Table I). Subsequently, the crabs frequently climbed onto the shells with their abdomen in full contact with the hydroid's polyps, but again, no evidence of stinging was observed (although some of the polyps did cling to sensory hairs on the abdomen). *Pagurus pollicaris* then lifted the lip of the shell off of the substrate with its chelipeds and placed its abdomen in the aperture of the shell and entered the shell. While the crab was entering the shell, no apparent stinging was observed.

TABLE I

The responses of naked Pagurus pollicaris, P. longicarpus, *and* Clibanarius vittatus *to initial contact with a hydroid-colonized shell*

Hermit crab	n	Initial contact elicits: Sting response	Initial contact elicits: No sting response	Chi-squared test: χ^2	Chi-squared test: *P*
P. pollicaris	10	0	10	10.0	<.01
P. longicarpus	10	9	1	6.4	<.05
C. vittatus	14	10	4	2.6	NS

Pagurus longicarpus also commonly made initial contact with the hydroid with its antennae, but usually responded as if stung by quickly jumping back several centimeters (Table I). Those crabs subsequently avoided any further contact with the shell.

Clibanarius vittatus also initially contacted the hydroid with its antennae, and, while most of the crabs reacted as if stung, some did not (Table I). Three of the crabs that showed no stinging response upon initial antennal contact climbed on top of the shell, as *P. pollicaris* did. At this time, all three of the crabs appeared to be stung and avoided further contact with the shell. Seven of the crabs did enter the shell in a manner similar to that of *P. pollicaris*, including some of the crabs that had apparently been stung upon initial antennal contact.

Cnida discharge tests

The average number of cnidae discharged onto sensory hairs pulled directly off of *P. pollicaris* in hydroid-colonized shells was 2.1 (S.D. = 1.3). The average number of cnidae on the sensory hairs of *P. pollicaris* that had been touched by one of the authors to the dactylozooid polyps was 9.4 (S.D. = 5.9). Significantly more cnidae discharged onto the sensory hairs of the latter group (T-test, $P < .005$) (see Fig. 2). In addition, cnidae also discharged onto the sensory hairs of *C. vittatus* that were touched by one of the authors to the dactylozooid polyps (mean = 8.2, S.D. = 5.6) (see Fig. 3).

Shell preference tests

Experiment 1. Table II summarizes the results of the experiment in which the naked hermit crabs were given a choice between hydroid-colonized shells and bare shells.

The shell types occupied by *Pagurus pollicaris* from the FSUML were random after five minutes, but after eight hours bare shells had been chosen more frequently. Eleven shell switches occurred between the two observations. Although eight of the eleven shell switches involved the crab's switching from shells with a hydroid to bare shells, this ratio is not significantly different from random.

Pagurus pollicaris from St. Joseph Bay differed from their FSUML conspecifics in shell choice after both five minutes and eight hours. *Pagurus pollicaris* from St. Joseph Bay had chosen shells with hydroids more frequently after five minutes, but after eight hours the shell types occupied did not differ from random. Thirteen shell switches occurred between the two observations. Ten of the 13 switches ($P = .06$) involved the crabs' switching from a shell with a hydroid to a bare shell.

The shell types occupied by both populations of *P. longicarpus* from the FSUML and St. Joseph Bay were random after five minutes, but bare shells had been chosen much more frequently after eight hours ($P < .001$, for the pooled data from both populations). Five switches occurred between the two observations for the crabs from the FSUML. Four of the five switches (not significant) involved the crabs' switching from hydroid-colonized shells to bare shells. Only two switches occurred with the crabs from St. Joseph Bay, both from hydroid-colonized shells to bare shells. Overall,

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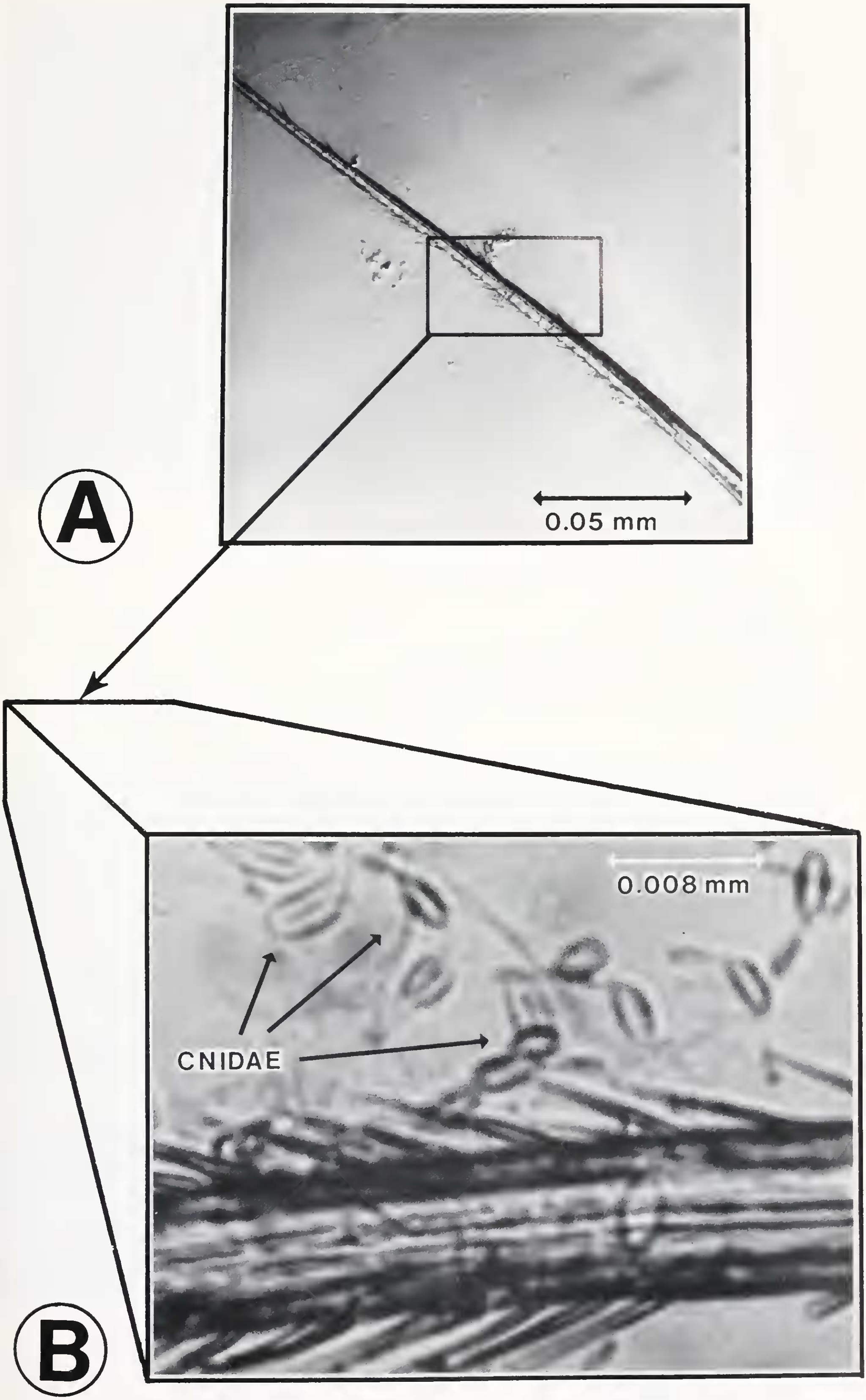
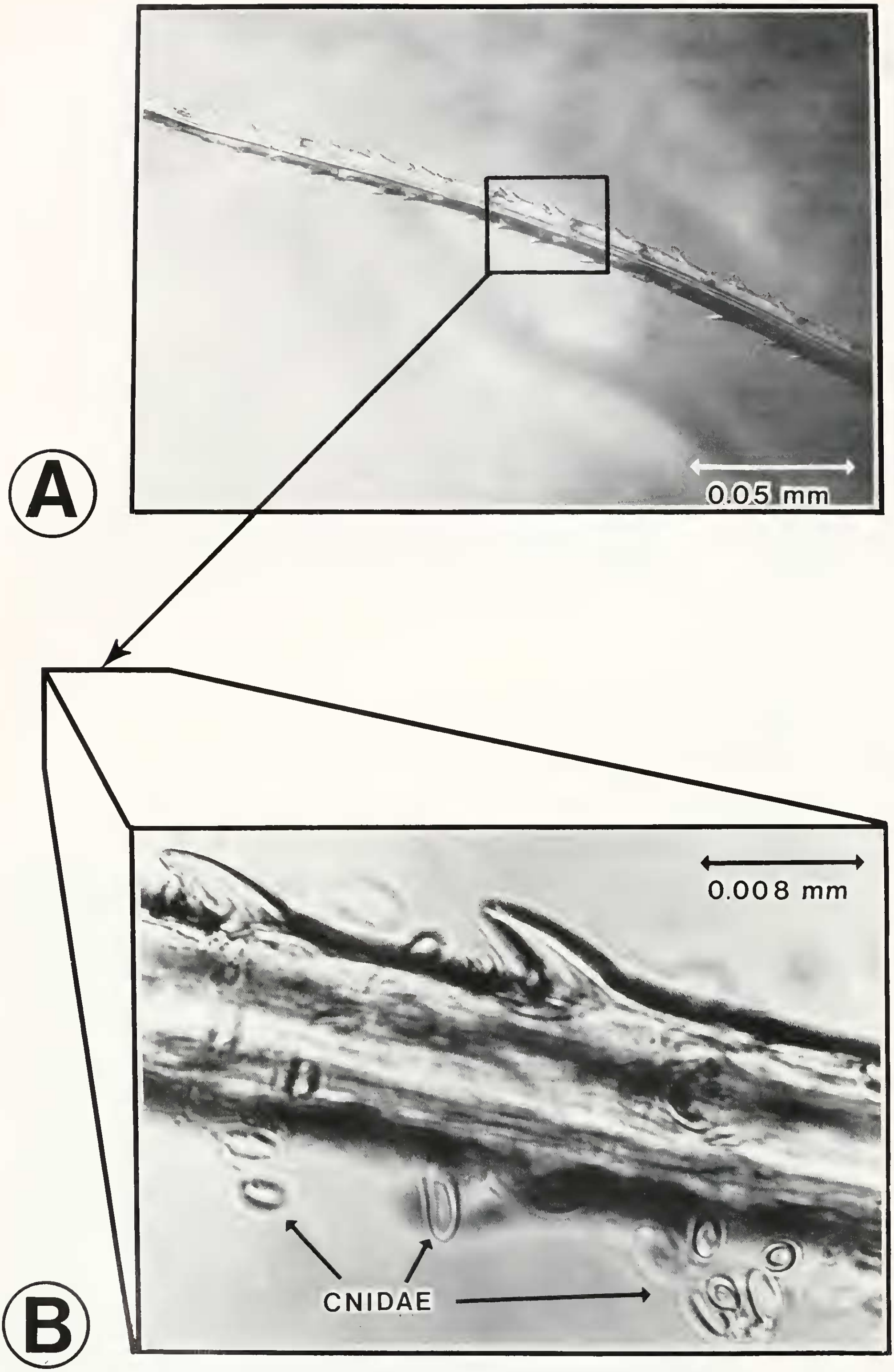
FIGURE 2. A sensory hair from the carpus of *Pagurus pollicaris,* shown before (A) and after (B) being rubbed along the fringe of dactylozooid polyps of the hydroid colony. Notice the numerous discharged cnidae on the sensory hair that has been touched to the hydroid.


A
0.05 mm
B
0.008 mm
CNIDAE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seven switches occurred, six of them involving the crabs' vacating hydroid-colonized shells ($P = .07$, for the pooled data of the two populations at both observations).

Both populations of *C. vittatus* had chosen bare shells much more frequently than hydroid-colonized shells after five minutes and after eight hours ($P < .01$, for the pooled data of the two populations after both observation periods). No shell switches occurred between the two observations.

Control 1. In this experiment, the naked hermit crabs were given a choice between shells that had had their hydroid colony scraped off and bare shells.

The shell types occupied by each population of *P. pollicaris, P. longicarpus,* and *C. vittatus* were random after both observation periods. The pooled data for the two populations of *P. pollicaris* shows that after five minutes 26 out of 53 hermit crabs had chosen scraped shells, and after eight hours 29 out of 60 had chosen scraped shells. The pooled data for the two populations of *P. longicarpus* shows that after five minutes 7 out of 19 hermit crabs had chosen scraped shells, and after eight hours 8 out of 19 had chosen scraped shells. The pooled data for the two populations of *C. vittatus* shows that after five minutes 11 out of 18 had chosen scraped shells, and after eight hours 14 out of 27 had chosen scraped shells. No shell switches occurred between the two observations.

Experiment 2. Table III summarizes the results of the experiment in which the naked crabs were first allowed to enter shells in which only their abdomens could fit and then given a choice between hydroid-colonized shells and bare shells.

Only 12 of the 20 *P. pollicaris* from the FSUML had chosen a shell after five minutes. Nine of the 12 shells chosen were bare shells (not significant), but after eight hours all 20 crabs had chosen a shell, and 16 of them were bare shells ($P < .01$). No shell switches occurred between the two observations.

Although *P. pollicaris* from St. Joseph Bay occupied shells randomly after both observation periods, it appears that after eight hours there is a trend toward bare shells (14 of 22 shells chosen were bare shells). Only two shell switches occurred, both from shells with a hydroid to bare shells.

The pooled data from the two populations of *P. pollicaris* indicate that after five minutes the shell types occupied were random, but after eight hours bare shells had been chosen more frequently.

Each population of *P. longicarpus* and *C. vittatus* had selected bare shells more frequently at both observations. A total of only three shell switches (all from shells with hydroids to bare shells) occurred between observations for both hermit crab species.

Control 2. In this experiment, the naked crabs were first allowed to enter shells in which only their abdomens could fit and then given a choice between shells that had had their hydroid colony scraped off and bare shells.

The shell types occupied by each population of *P. pollicaris, P. longicarpus,* and *C. vittatus* were random at both observations. The pooled data for the two populations of *P. pollicaris* shows that after five minutes 14 out of 33 hermit crabs had chosen scraped shells, and after eight hours 17 out of 39 had chosen scraped shells. The pooled data for the two populations of *P. longicarpus* shows that after five minutes 10 out of 19 hermit crabs had chosen scraped shells, and after eight hours 11 out of 20 had chosen scraped shells. The pooled data for the two populations of *C. vittatus*

FIGURE 3. A sensory hair from the carpus of *Clibanarius vittatus,* shown before (A) and after (B) being rubbed along the fringe of dactylozooid polyps of the hydroid colony. Notice the numerous discharged cnidae on the sensory hair that has been touched to the hydroid.

TABLE II

Results of shell-selection tests of naked Pagurus pollicaris, P. longicarpus, *and* Clibanarius vittatus *from two localities: hydroid-colonized shells* versus *shells without hydroids**

Hermit crab	Locality	No. tested	Time of observation	No. selecting shells				No. switching shells between 5 min and 8 h, from		Chi-squared test	
				With hydroid	Without hydroid	χ^2	P	With hydroid to without hydroid	Without hydroid to with hydroid	χ^2	P
P. pollicaris	FSUML	30	5 min	15	14	0.03	NS	8	3	2.27	NS
			8 h	9	21	4.80	<.05				
P. pollicaris	St. Joseph Bay	30	5 min	21	7	7.00	<.01	10	3	3.77	NS (p = .06)
			8 h	15	15	0.00	NS				
P. pollicaris	Pooled	60	†					18	6	6.00	<.05
			†								
P. longicarpus	FSUML	10	5 min	5	5	0.00	NS	4	1	1.80	NS
			8 h	1	9	6.40	<.05				
P. longicarpus	St. Joseph Bay	10	5 min	2	4	0.67	NS	2	0	2.00	NS
			8 h	1	9	6.40	<.05				
P. longicarpus	Pooled	20	5 min	7	9	0.25	NS	6	1	3.57	NS (P = .07)
			8 h	2	18	12.80	<.001				
C. vittatus	FSUML	20	5 min	1	9	6.40	<.05	0	0		
			8 h	1	18	15.21	<.001				
C. vittatus	St. Joseph Bay	10	5 min	2	6	2.00	NS	0	0		
			8 h	0	10	10.00	<.01				
C. vittatus	Pooled	30	5 min	3	15	8.00	<.01	0	0		
			8 h	1	28	25.14	<.001				

* "Pooled" means that the results from the two populations of hermit crabs have been combined.

† Pooling inappropriate because of differences in shell selection between the two populations.

TABLE III

Results of shell-selection tests of Pagurus pollicaris, P. longicarpus, *and* Clibanarius vittatus *(all from two localities) who were first allowed to enter shells in which only the abdomen could fit: hydroid-colonized shells* versus *shells without hydroids**

Hermit crab	Locality	No. tested	Time of observation	No. selecting shells		χ^2	P	No. switching shells between 5 min and 8 h, from		Chi-squared test	
				With hydroid	Without hydroid			With hydroid to without hydroid	Without hydroid to with hydroid	χ^2	P
P. pollicaris	FSUML	20	5 min	3	9	3.00	NS	0	0		
			8 h	4	16	7.20	<.01				
P. pollicaris	St. Joseph Bay	22	5 min	10	11	0.05	NS	2	0	2.00	NS
			8 h	8	14	1.64	NS				
P. pollicaris	Pooled	42	5 min	13	20	1.48	NS	2	0	2.00	NS
			8 h	12	30	7.77	<.01				
P. longicarpus	FSUML	10	5 min	3	5	0.11	NS	1	0	1.00	NS
			8 h	2	8	3.60	NS (P = .06)				
P. longicarpus	St. Joseph Bay	10	5 min	1	7	4.50	<.05	1	0	1.00	NS
			8 h	1	9	6.40	<.05				
P. longicarpus	Pooled	20	5 min	4	12	4.00	<.05	2	0	2.00	NS
			8 h	3	17	9.80	<.01				
C. vittatus	FSUML	17	5 min	0	14	14.00	<.001	0	0		
			8 h	0	17	17.00	<.001				
C. vittatus	St. Joseph Bay	10	5 min	1	8	5.44	<.05	1	0	1.00	NS
			8 h	0	10	10.00	<.01				
C. vittatus	Pooled	27	5 min	1	22	19.17	<.001	1	0	1.00	NS
			8 h	0	27	27.00	<.001				

* "Pooled" means that the results from the two populations of hermit crabs have been combined.

show that after five minutes 12 out of 23 hermit crabs had chosen scraped shells, and after eight hours, 14 out of 26 had chosen scraped shells. No shell switches occurred between the two observations.

Experiment 3. In this experiment, the naked crabs were given a single hydroid-colonized shell.

The majority of *P. pollicaris* from the FSUML and St. Joseph Bay populations entered the hydroid-colonized shells. The pooled data show that after five minutes 18 of 20 crabs had entered the shell ($P < .001$), and after eight hours all 20 had entered the shell ($P < .001$).

Only some *P. longicarpus* from both populations had entered the hydroid-colonized shell after five minutes (7 of 20, random success-failure rate). The pooled data after eight hours, however, show that 19 of 20 ($P < .001$) *P. longicarpus* entered the shell.

Only 1 of 24 ($P < .001$) *C. vittatus* from both populations had entered the hydroid-colonized shell after five minutes. The pooled data after eight hours, however, show that 10 of 24 (random success-failure rate) *C. vittatus* entered the shell.

Experiment 4. Table IV summarizes the results of the experiment in which, in the presence of a stone crab, *M. mercenaria,* the naked hermit crabs were given a choice between hydroid-colonized shells and bare shells.

Sixteen of 24 (not significant) *P. pollicaris* from the FSUML had chosen bare shells after five minutes, and after eight hours 18 of 22 ($P < .01$) had chosen bare shells. Two *P. pollicaris* in bare shells were killed by *M. mercenaria* sometime between the two observations. Four shell switches occurred, all from hydroid-colonized shells to bare shells ($P < .05$).

The shell types occupied by *Pagurus pollicaris* from St. Joseph Bay were random after both observation periods. Again, two *P. pollicaris* in bare shells were killed by the stone crab. No switches occurred between the two observations.

The shell types occupied by both populations of *P. longicarpus* were random after five minutes, but 20 of 24 ($P < .01$) crabs had chosen bare shells after eight hours. Seven *P. longicarpus,* all in bare shells, were killed by the stone crab. Four of the crabs killed were from St. Joseph Bay, and the remainder from the FSUML.

Clibanarius vittatus was not tested in this experiment.

Experiment 5. Table V summarizes the results of the experiment in which the naked hermit crabs were given a choice between hydroid-colonized shells and bare shells in the presence of the octopus *O. joubini.*

The shell types occupied by *Pagurus pollicaris* from the FSUML were random after five minutes, but after eight hours 17 of 20 ($P < .01$) crabs had chosen bare shells more frequently. One *P. pollicaris* in a bare shell was killed by the octopus. Three shell switches occurred, all from hydroid-colonized shells to bare shells (not significant).

The shell types occupied by *Pagurus pollicaris* from St. Joseph Bay were random after both observation periods. Again, one *P. pollicaris* in a bare shell was killed by the octopus. Three shell switches occurred, all from hydroid-colonized shells to bare shells (not significant).

The shell types occupied by both populations of *P. longicarpus* were random after five minutes, but 32 of 35 ($P < .001$) crabs had chosen bare shells after eight hours. One FSUML *P. longicarpus* in a bare shell was killed by the octopus. Seven shell switches occurred (all from shells with hydroids to bare shells, $P < .01$) between the observations by both hermit crab species. Four of the seven switches occurred by the St. Joseph Bay crabs, and the remainder from the FSUML.

Clibanarius vittatus was not tested in this experiment.

TABLE IV

Results of shell-selection tests of naked Pagurus pollicaris *and* P. longicarpus *from two localities: hydroid-colonized shells versus shells without hydroids in the presence of* Menippe mercenaria*

Hermit crab	Locality	No. tested	Time of observation	No. selecting shells: With hydroid	No. selecting shells: Without hydroid	χ^2	*P*	No. switching shells between 5 min and 8 h, from: With hydroid to without hydroid	No. switching shells between 5 min and 8 h, from: Without hydroid to with hydroid	Chi-squared test: χ^2	Chi-squared test: *P*
P. pollicaris	FSUML	24	5 min	8	16	2.67	NS	4	0	4.00	<.05
			8 h	4	18	8.91	<.01			(2 killed)	
P. pollicaris	St. Joseph Bay	18	5 min	6	12	2.00	NS	0	0	(2 killed)	
			8 h	6	8	0.29	NS				
P. pollicaris	Pooled	42	5 min	†				4	0	4.00	<.05
			8 h	†							
P. longicarpus	FSUML	17	5 min	5	12	2.88	NS	2	0	2.00	NS
			8 h	2	12	7.14	<.01			(3 killed)	
P. longicarpus	St. Joseph Bay	14	5 min	6	8	0.29	NS	1	0	1.00	NS
			8 h	2	8	3.60	NS ($P = .06$)			(4 killed)	
P. longicarpus	Pooled	31	5 min	11	20	2.61	NS	3	0	3.00	NS
			8 h	4	20	10.67	<.01				

* "Pooled" means that the results from the two populations of hermit crabs have been combined.

† Pooling inappropriate because of differences in shell selection between the two populations.

TABLE V

Results of shell-selection tests of naked Pagurus pollicaris *and* P. longicarpus *from two localities: hydroid-colonized shells* versus *shells without hydroids in the presence of* Octopus joubini*

				No. selecting shells				No. switching shells between 5 min and 8 h, from		Chi-squared test	
Hermit crab	Locality	No. tested	Time of observation	With hydroid	Without hydroid	χ^2	P	With hydroid to without hydroid	Without hydroid to with hydroid	χ^2	P
P. pollicaris	FSUML	21	5 min	7	14	2.33	NS	3	0	3.00	NS
			8 h	3	17	9.80	<.01			(1 killed)	
P. pollicaris	St. Joseph Bay	18	5 min	10	6	1.00	NS	3	0	3.00	NS
			8 h	8	9	0.06	NS			(1 killed)	
P. pollicaris	Pooled	39	5 min	†				6	0	6.00	<.05
			8 h	†							
P. longicarpus	FSUML	15	5 min	3	9	3.00	NS	3	0	3.00	NS
			8 h	0	14	14.00	<.001			(1 killed)	
P. longicarpus	St. Joseph Bay	21	5 min	8	11	0.22	NS	4	0	4.00	<.05
			8 h	3	18	10.71	<.01				
P. longicarpus	Pooled	36	5 min	7	24	9.32	<.01	7	0	7.00	<.01
			8 h	3	32	24.01	<.001				

* "Pooled" means that the results from the two populations of hermit crabs have been combined.

† Pooling inappropriate because of differences in shell selection between the two populations.

DISCUSSION

When an organism's habitat selection is studied, it is important to consider the factors associated with the habitat that will affect the survival of the organism. In the present study, the effect of a hydroid colony on the shell selection behavior of three species of hermit crabs was investigated. But of what value is a hydroid colony to these or other crabs? Schifjsma (1935) suggested that the hydroid constantly enlarges the volume of the shell by growing outward on the lip of the shell. Grant and Pontier (1973) and Brooks and Mariscal (in prep.) have shown that a hydroid-colonized shell protects *Pagurus* from predatory crabs and octopuses. Grant and Pontier (1973) have also shown that *P. acadianus* inhabiting hydroid-colonized shells were dominant over similar-sized crabs in bare shells in 74% of the trials. In addition, Wright (1973) and Grant and Ulmer (1974) have suggested that competition between sympatric species for shells may be lessened because some species reject shells covered with a hydroid.

Regardless of the proposed advantages of inhabiting hydroid-colonized shells, nearly all of the hermit crabs in the present study chose bare shells under all of the experimental conditions. In fact, if the crabs did choose hydroid-colonized shells after five minutes, they frequently vacated these shells for bare shells during the remainder of the trial, even when predatory crabs and octopuses were present. Interestingly, *O. joubini* activates the anemone-transferring behavior of *P. pollicaris* towards its symbiotic sea anemone, *Calliactis tricolor* (Brooks and Mariscal, in prep.), which provides some protection from octopuses (McLean, 1983). Neither the octopus nor the stone crab, however, stimulated the hermit crabs to select hydroid-colonized shells, which also provide protection (Brooks and Mariscal, in prep.).

One population of *P. pollicaris*, from St. Joseph Bay, chose hydroid-colonized shells more frequently in one trial. Seventy-five percent of the *P. pollicaris* from St. Joseph Bay inhabited hydroid-colonized shells after five minutes in Experiment 1, compared with only 52% of *P. pollicaris* from the FSUML in the same experiment. This difference in shell selection between these two populations corroborates the discovery by Brooks and Mariscal (in prep.) that *P. pollicaris* from St. Joseph Bay are more active in acquiring the sea anemone *C. tricolor* than *P. pollicaris* from the FSUML. These populational differences observed in *P. pollicaris* may be due to differences in selective pressures between the two localities. For example, differences in predation pressure (*cf.*, Bertness, 1982) may affect the behavior of hermit crabs toward the hydroid-colonized shells and possibly account for the shell selection descrepancies reported in the literature for both *P. pollicaris* and *P. longicarpus*. The hermit crabs from St. Joseph Bay inhabit areas with more *O. joubini* than those crabs from the FSUML (pers. obs.). Therefore, the St. Joseph Bay crabs may "prefer" hydroid-colonized shells for protection. This observation does not explain, however, why *P. pollicaris* from St. Joseph Bay generally switched from hydroid-colonized shells to bare shells, even in the presence of *O. joubini*.

Apparently, living in a hydroid-colonized shell has some disadvantages. The most likely disadvantage of inhabiting a hydroid-colonized shell is being stung by the hydroid's nematocysts. Of the three species of hermit crab tested in this study, only *P. pollicaris* appeared unaffected by contact with the hydroid. There were, however, discharged nematocysts on the sensory hairs of *P. pollicaris* before and after their being manually touched to the dactylozooid polyps. Although *P. pollicaris* did not react as if stung, it presumably could still be affected by the discharged nematocysts. Perhaps *P. pollicaris* subsequently switch out of hydroid-colonized shells to avoid the lashing dactylozooid polyps, which appear to contact the hermit crab repeatedly. Wright (1973) reported that four *P. pollicaris* switched from hydroid-colonized shells to bare shells, but two of the crabs soon returned to their former shells. In the studies by Wright (1973), Conover (1976), and Mercando and Lytle (1980), where *P. pollicaris* preferred hydroid-colonized shells, the selective pressures (*e.g.*, predation or competition for shells) on each population may have been too great for the crabs to vacate their shells normally in favor of bare shells.

Although all three hermit crab species in this study preferred bare shells, if given no other choice they would enter hydroid-colonized shells. Wright (1973) reported that only one *C. vittatus* entered a hydroid-colonized shell and soon began to pick off all of the polyps it could reach until the polyps could not reach the crab. A total of 23 *C. vittatus* entered hydroid-colonized shells in the present study, but none was observed picking at the hydroid colony.

The *P. pollicaris*, *P. longicarpus*, and *C. vittatus* collected in the present study are all sympatric. Wright (1973) has suggested that because *C. vittatus*, a competitive dominant over both *P. pollicaris* and *P. longicarpus*, usually avoids hydroid-colonized shells, competition for shells between these three species is reduced. In the present study, both *C. vittatus* and *P. longicarpus* rejected hydroid-colonized shells more frequently than *P. pollicaris*. The effect of this difference on shell competition between these crabs is unclear. *Clibanarius vittatus* from the FSUML were usually found in *Melongena corona* shells (which rarely have hydroids), whereas similar-sized *Pagurus* from the same localities usually inhabit *Polinices duplicatus* shells, which often bear hydroid colonies (pers. obs.). Therefore, if *C. vittatus* prefers different shell species in this area, then its rejection of hydroid-colonized *P. duplicatus* shells probably has little effect on its interactions with *Pagurus*. *Clibanarius vittatus* from St. Joseph Bay, however, were commonly found in *P. duplicatus* shells, as were similar-sized *Pagurus* (pers. obs.). In St. Joseph Bay, competition for shells between *C. vittatus* and *P. pollicaris* may be reduced because of differences in the selection of hydroid-colonized shells.

The occupation of a hydroid-colonized shell can potentially provide hermit crabs with certain benefits. Predation levels can be minimized, fitness increased, and competition with other shell-seeking hermit crabs reduced. Certain hermit crabs, however, still prefer bare shells to hydroid-colonized shells. Apparently, those hermit crabs that select hydroid-colonized shells are either not stung or tolerant of the hydroid's cnidae. Nonetheless, the preference for hydroid-colonized shells implies that the benefits of inhabiting this shell are greater than the harmful consequences.

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